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Citation for published version:
Rowland, L, da Costa, ACL, Galbraith, DR, Oliveira, RS, Binks, OJ, Oliveira, AAR, Pullen, AM, Doughty, CE, Metcalfe, DB, Vasconcelos, SS, Ferreira, LV, Malhi, Y, Grace, J, Mencuccini, M & Meir, P 2015, 'Death from drought in tropical forests is triggered by hydraulics not carbon starvation', *Nature*, vol. 528, no. 7580, pp. 119–122. https://doi.org/10.1038/nature15539

Digital Object Identifier (DOI):
10.1038/nature15539

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Peer reviewed version

Published In:
Nature

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Download date: 08. May. 2023

Long-term tropical forest drought: death triggered by hydraulics, not carbon starvation

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Drought and warming threaten tropical rainforests over seasonal to decadal timescales[1-4]. The drivers of tree mortality following drought remain poorly understood[5], particularly in tropical ecosystems[6]. During severe drought, reduced availability of non-structural carbohydrates (NSC) has been hypothesised to critically increase mortality risk through insufficient carbon supply to metabolism ('carbon starvation')[7,8]. However little is known about how NSC stores are affected by drought, especially over the long term, and whether they are more important than hydraulic processes in controlling drought-induced mortality. Using data from the

world's longest running experimental drought study in tropical rainforest we present new insights into whether carbon starvation or deterioration of the water conducting pathways from soil to leaf trigger tropical tree mortality during decadal-scale drought. Biomass loss from mortality in the experimentally droughted forest increased substantially after >10 years of reduced soil moisture availability. The mortality signal is dominated by the death of large trees, which we show are at a much greater risk of hydraulic deterioration than smaller trees. However, we find no evidence that the droughted trees suffered carbon-starvation, as growth rates were maintained or elevated in both surviving and dying individuals, and NSC concentrations were not significantly different from those in non-droughted trees.

Drought-response observations from both field-scale experiments and natural droughts have demonstrated increased mortality over the short-term (1-3 years), with notably higher vulnerability for some taxa, and for larger trees[6,9,10]. After several years of drought, recovering growth rates in smaller trees, dbh (diameter at breast height) <40 cm, and reduced mortality have been recorded at different locations[6,11,12]. However, the long-term (>10 yr) sensitivity of tropical forests to predicted prolonged and repeated water deficit[1-3] and the physiological mechanisms influencing this are poorly understood. Through-fall exclusion (TFE) studies, that create soil moisture deficit by the exclusion of a fraction of incoming rainfall, provide the only current means to assess the long-term response in mechanistic detail[5,13].

Trees experiencing drought stress are thought to die from direct physiological failure and/or from injury and biotic attack associated with a decline in physiological vigour[14]. A global effort to identify the relevant physiological mechanisms triggering death and thus to improve predictions of forest tree mortality has focussed on the twin possibilities of: (i) failure to

supply sufficient carbon substrate to metabolism following drought-related reductions in photosynthesis and increased use of NSC, theoretically leading to carbon starvation; and (ii) deterioration of the water-conducting xylem tissue, causing a rapid or gradual failure of key functional processes (e.g. photosynthesis and phloem transport), to trigger sufficient desiccation of the meristematic tissues[14,15], ultimately leading to mortality. Despite recent intensive research, it is unclear how important these two mechanisms are in different biomes and how, or whether, to model them[16].

Since 2002 a 50% TFE treatment has been implemented at a 1 ha-scale drought experiment in old-growth forest at Caxiuanã National Forest Reserve, Pará State, Brazil[6,12], to simulate possible rainfall reductions predicted to occur in parts of Amazonia by 2100[1]. Mortality surveys, recruitment and growth rates of all trees ≥10 cm dbh, have been monitored through the experimental period (see Methods). Recently, seasonal data on NSC concentrations were measured on leaves, branches and stems of 41 trees (20 trees on the control, 21 trees on the TFE) of the most common genera in the experiment (Extended Data Table 1). Xylem vulnerability curves were also performed on the branches of these trees (see Methods). Here, we synthesise these data to test whether long-term soil moisture deficit alters NSC storage and use in tropical rainforest trees, and if this, or hydraulic processes, are most strongly associated with increased mortality rates.

By 2014, following 13 years of the TFE treatment, cumulative biomass loss through mortality was 41.0±2.7% relative to pre-treatment values (Fig. 1a), and the rate of loss had increased substantially since the previous reported value of 17.2±0.8%, after 7 years of TFE[6]. Accelerating biomass loss and failure to recover substantially, or to reach a new equilibrium[13], has led to a committed flux to the atmosphere from decomposing necromass of 101.9±19.1 Mg C ha^{-1} (Fig. 1a). This biomass loss has been driven by elevated mortality in

72 the largest trees (Fig. 1b), as previously observed over shorter timescales[6], and has created a
73 canopy that has had a persistently lower average leaf area index during 2010-2014
74 (12.0±1.2% lower; Extended data Fig. 1).

75 Remarkably, individual tree growth rates for the four years prior to death showed no
76 significant reduction in either the TFE or control plots (Fig. 2a), indicating that growth is
77 prioritised to the point of death irrespective of the soil moisture deficit treatment. From 2008,
78 tree growth in every wet season (January-June) on the TFE treatment relative to the control
79 was significantly elevated (P<0.05) in the small and medium trees (up to 4.6±0.2 times
80 higher in small trees, and 2.9±0.2 times higher in medium trees), and maintained in the
81 largest trees (10-20 cm, 20-40 cm and >40 cm dbh, respectively; Fig. 2b-d). Elevated wet
82 season growth occurred despite 0.1-0.9 MPa reduction in average soil water potential (Ψ_s) at
83 depths of 0-4 m on the TFE and a loss of seasonality in Ψ_s (Extended Data Fig. 2). Increased
84 growth in the small trees occurred from 2008 onwards, following earlier substantial mortality
85 of large trees (Fig. 1), which generated canopy gaps. Increased light availability to smaller
86 trees, and presumably reduced below-ground competition for water and nutrients, allowed
87 competitive release of trees on the TFE[8], and elevated growth rates. Competitive release on
88 the TFE implies that, following 13 years of drought-stress, photosynthetic production is
89 sufficient not only to maintain growth in the largest trees (Fig. 2d), but to increase growth in
90 trees <40 cm dbh (Fig. 2b-c). This response would not be possible if the majority of trees
91 were severely carbon limited, unless very considerable long-term (or renewed) carbon
92 resources were being drawn upon.

93 Prioritisation of growth under drought in the TFE is consistent with recent observations
94 following short-term drought in Amazonia[7]. However, the maintenance of NSC
95 concentrations in the TFE treatment suggests that the prioritisation of growth during drought

does not occur at the expense of depleted carbon stores, as previously hypothesised[7]. Neither the concentrations of soluble sugar (carbon immediately available to metabolism) nor starch (stored carbon which can be converted to sugars) were significantly depleted in stem, leaf and branch tissue from the TFE, relative to control (Fig. 3). The seasonal changes in both sugar and starch concentrations, which varied by 50-90%, were much larger than any differences associated with the TFE treatment (Fig. 3). Despite 13 years of severely reduced soil moisture availability, the seasonal cycle and use of NSCs was unaltered, implying that the sampled trees did not draw significantly upon their NSC reserves to buffer against the long-term effects of soil moisture deficit. Large shifts in carbon allocation to roots and leaves, which could compensate for drought-induced changes in carbon investment in stem growth if photosynthesis is reduced[17], have not been reported on the TFE[12], and similarly no drought-induced change in photosynthetic capacity has occurred[18]. Considering this and additional evidence of no increase in herbivore attack on the TFE (Extended Data Fig. 3), our results suggest progressive carbon starvation and biotic foliar consumption are not important drivers of the mortality patterns observed in the TFE forest following extended severe soil moisture deficit (>10 years).

Deterioration of the water transport system in the xylem tissues following drought can also lead to death[17,19]. The vulnerability of the xylem to drought is described by a vulnerability curve[20], which relates water potential in xylem conduits to loss of hydraulic conductivity because of occlusions by gas emboli. The water potential at which 50% loss of xylem conductivity occurs ($P_{50,}$ MPa) is a commonly used index of embolism resistance[20]. We determined xylem P_{50} for the trees on the control and TFE plots, with tree dbh ranging from 15 to 48 cm. A highly significant decrease in P_{50} with dbh was found across TFE and control (Extended Data table 3, $P<0.01$). As dbh increased from 15 to 48 cm there was a 1.3±0.2 MPa reduction in the P_{50} value, with significant genus-to-genus differences (Fig.4). Leaf

121 water potential (Ψ_l) could only be measured during limited sampling campaigns (2-3 days)
122 that were characterised by low vapour pressure deficit (VPD, 54-59% of peak dry season
123 values) and unseasonal rainfall in the preceding days. Differences between treatment and
124 control Ψ_l were not detected. Mean Ψ_l recorded across all the trees together with the
125 vulnerability curves determined for each genus were used to predict the percentage loss of
126 xylem conductivity (PLC) with dbh. Values of PLC at mean Ψ_l increased with dbh, with the
127 largest diameter trees predicted to have reductions in conductive capacity of about 80% in
128 some genera, indicating significant vulnerability to hydraulic deterioration (inset of Fig. 4).

129 Given no evidence of carbon starvation and similar Ψ_l across plots in the sample dates, why
130 did many more trees die in TFE than control? The lack of treatment differences in Ψ_l
131 contrasts starkly with the long-term records of lower Ψ_s, (Extended Data Fig. 2). The lack of
132 difference in midday Ψ_l could have been caused by sampling constraints or by isohydric
133 behaviour. We found little isohydric behaviour in our diurnal Ψ_l measurements (Extended
134 Data Fig. 4), with overall strong linear declines in Ψ_l observed with increasing VPD on the
135 control (R^2=0.18, P<0.01) and in particular on the TFE (R^2=0.33, P<0.01). Consequently
136 limited sampling is the most likely cause of equal Ψ_l between the two plots, with TFE trees
137 likely having more negative Ψ_l and lower hydraulic conductance during VPD maxima in the
138 dry season. Reduced carbon uptake because of stomatal closure in some TFE trees is
139 possible[21], but unlikely to have caused carbon starvation considering growth rates were
140 maintained or elevated on the TFE (Fig. 2) and radial growth is considered more sensitive to
141 drought stress than photosynthetic processes[22]. Strongly reduced Ψ_s on the TFE (Extended
142 Data Fig. 2) and significant hydraulic vulnerability of the tall trees are consistent with the
143 hypothesis of hydraulic deterioration as the most likely trigger of greater mortality,
144 particularly in the largest trees, as observed. Taller trees are predisposed to greater hydraulic

stress, from elevated atmospheric demand and longer hydraulic path lengths[23]. As the canopies are exposed to rainfall in the TFE, smaller trees might avoid meristematic desiccation[15] through leaf water uptake[24-26], but this may not be sufficient to save the largest trees, which we hypothesise are forced to maintain their high growth rates until death to continually replace dysfunctional xylem.

Following decadal-scale soil moisture depletion, our results suggest tropical rainforests will experience accelerating biomass loss and a likely transition to a lower statured, lower biomass forest state, due to substantially elevated mortality of the largest trees. This mortality is most likely triggered by hydraulic processes, which lead to hydraulic deterioration and limitations in carbon uptake[21], instead of being caused directly by carbon starvation. Under natural drought these forests may be under greater risk than from experimental drought, as severe soil moisture deficit is combined with low humidity and high air temperature increasing hydraulic demand. Improved prediction of the sensitivity of tropical tree mortality to drought should therefore focus on improved model simulation of plant hydraulics and modelling environmental controls on growth[27,22]. Decadal-scale ecological data such as these are rare, but they are invaluable for testing and improving vegetation model-based predictions over timescales relevant to climate change[28]. They also provide underpinning support for the long-term environmental policy needed to manage the natural capital that is embedded in tropical rainforests.

Author contributions

LR, PM, ALDC and MM designed and implemented the research. PM conceived and led the experiment and this study. LR led recent measurements; all authors contributed to data collection, led by ALDC. LR analysed the data with MM, PM, OB and AMP. LR wrote the paper with PM and MM, with contributions from all authors.

Acknowledgements:

This work is a product of UK NERC grant NE/J011002/1 to PM and MM, CNPQ grant 457914/2013-0/MCTI/CNPq/FNDCT/LBA/ESECAFLOR to ACLD, and ARC grant FT110100457 to PM. It was previously supported by NERC NER/A/S/2002/00487, NERC GR3/11706, EU FP5-Carbonsink and EU FP7-Amazalert to PM and JG, and by grant support to YM from NERC NE/D01025X/1 and the Gordon and Betty Moore Foundation. LR, MM and PM would also like to acknowledge support from Stephen Sitch, University of Exeter, and Yann Salmon, University of Helsinki, Finland.

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Fig. 1| Changes in biomass and mortality rates. a. Biomass on the control and TFE plot from 2002-2014 (Mg C ha^{-1} yr^{-1}). Error bars show the standard error calculated from 12 estimates of biomass, accounting for uncertainty in wood density and allometric equations (see Methods). b. Mortality rate (% stems $year^{-1}$) calculated separately for trees of 10-20 cm dbh, 20-40 cm dbh and >40 cm dbh on the control (black) and TFE (grey). The genus at date of death for each tree is shown in Extended data Table 2.

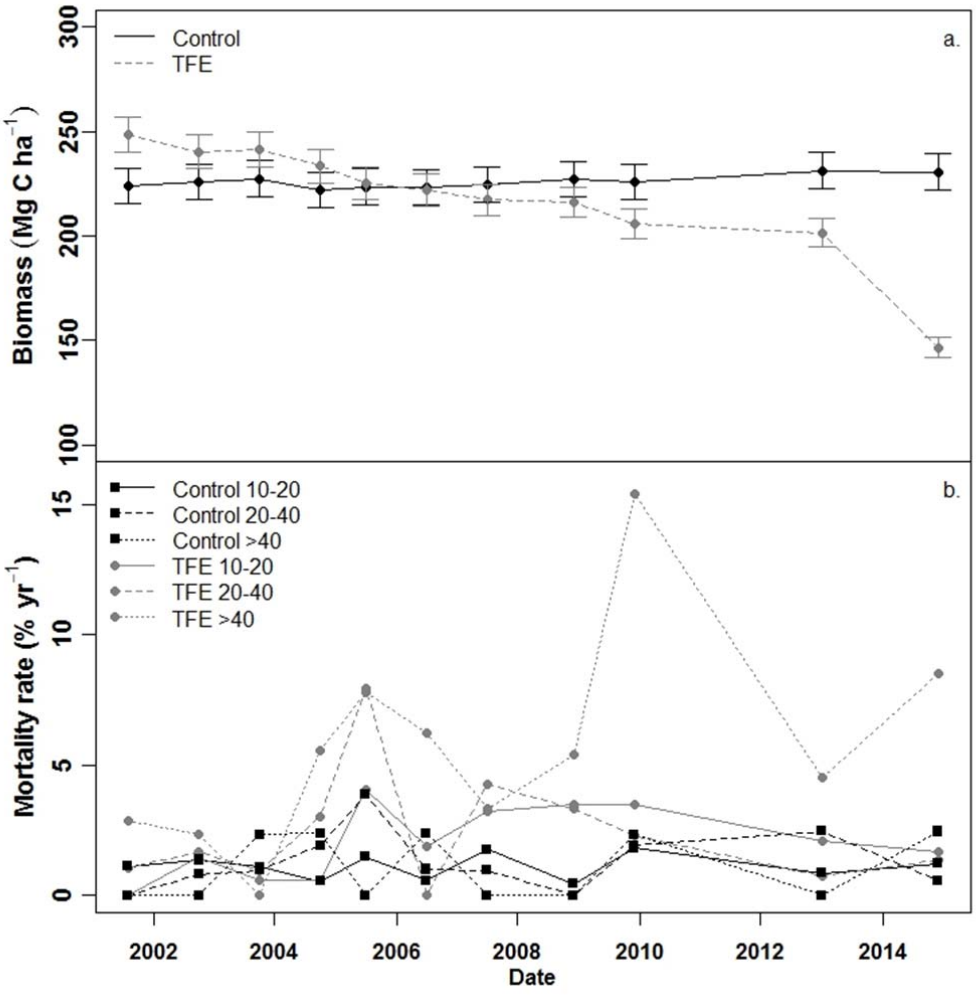


Fig. 2| Tree growth of living and dead trees. a. Average annual stem increment in the four years prior to death for all trees which died on the control (n=35) and TFE (n=60) from 2005 onwards. Growth rates are normalised by the growth in year 0, the year in which the tree died. b-d. Stem increment for small (a. 10-20 cm dbh), medium (b. 20-40 cm dbh) and large (c. >40 cm dbh) trees on the control and TFE plot from 2005 to 2014. Values for b-d are normalised by the maximum increment on the control plot. Error bars show the standard error.

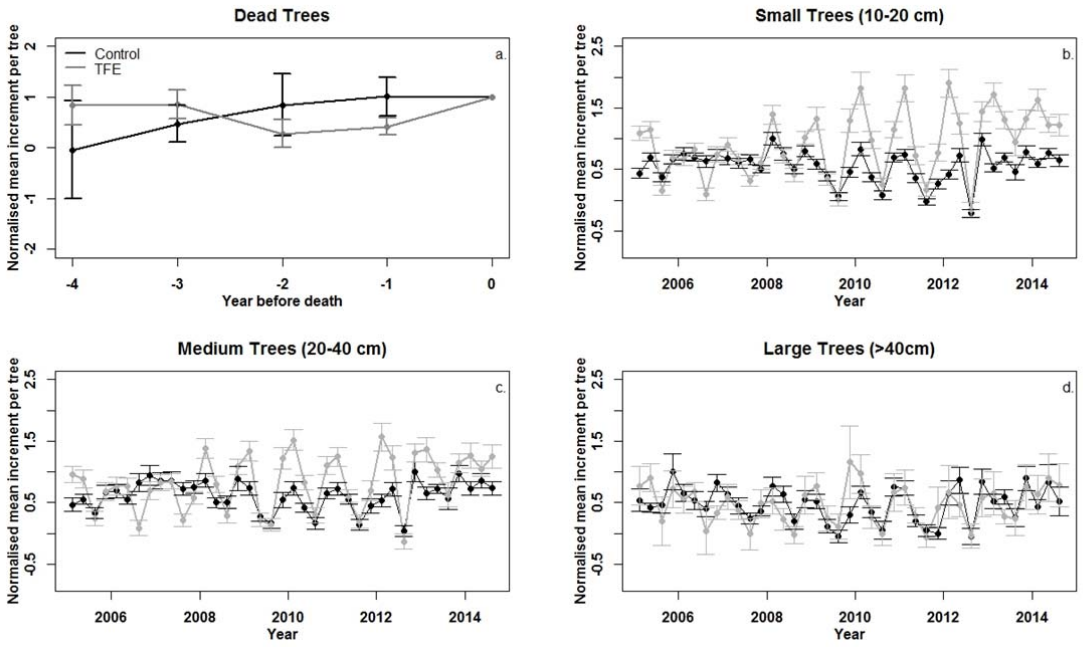


Fig. 3| Leaf, branch and stem NSC concentrations. Percentage values for soluble sugars (a.) and starch (b.) in dried biomass of leaves, branches and stems on the control and TFE for late dry season (November 2013), mid wet season (March 2014) and in the wet-to-dry transition (June 2014). Error bars show standard errors and * indicates a significant difference at $P < 0.05$. June 2014 has significantly elevated sugar values on the TFE plot, however the absolute values for sugar concentration are very low, and the absolute differences are very small.

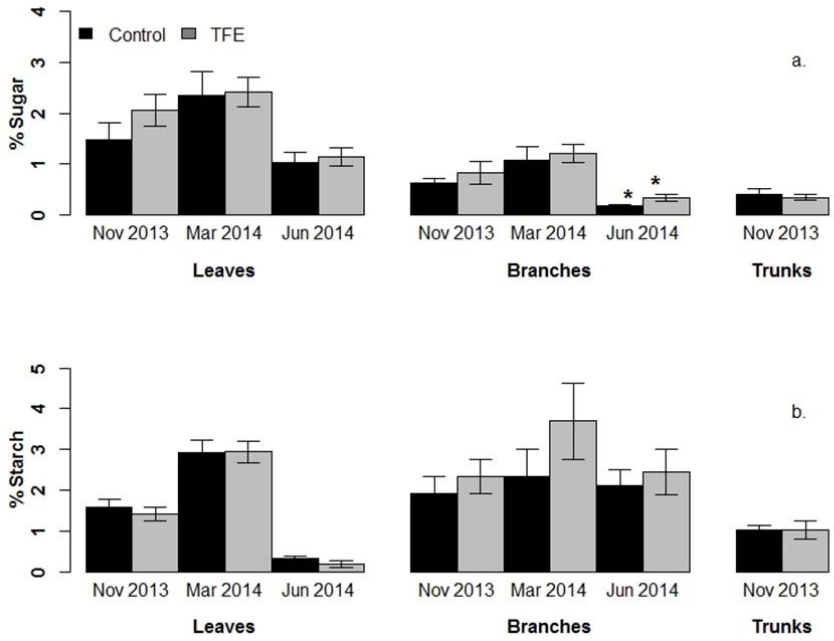
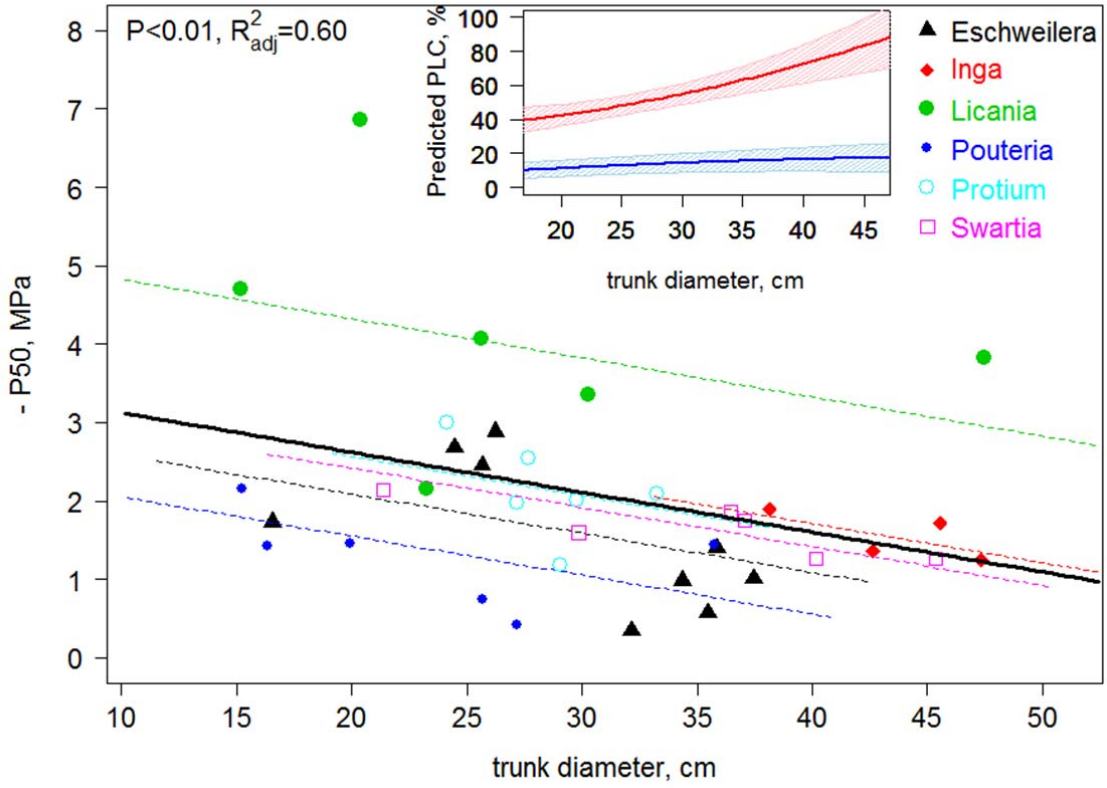


Figure 4| Xylem vulnerability to embolism and predicted loss of xylem hydraulic conductivity as a function of tree diameter (dbh). A general linear model was employed to test for the effects of genus and tree dbh on the estimates of xylem P_{50} obtained for each species. The dashed lines give the predicted regressions for each of the six genera, whereas the bold black line gives the overall mean regression line across all species (The adjusted R^2 in the figure refers to the overall model, while the P value refers to the significance of tree dbh). The insert shows the changes in predicted losses of hydraulic conductivity (PLC) as a function of tree size. In the main graph, each genus is represented with a different symbol and/or colour, as detailed in the legend. In the inset, the bold lines represent the average prediction for the most vulnerable genus (red: *Pouteria*) and for the most resistant one (blue: *Licania*) to drought induced embolism, with the shaded areas (pink, light blue) giving the respective 95% confidence intervals.



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